A NEW SPECIES OF THE HYRACOID MAMMAL *TITANOHYRAX* FROM THE EOCENE OF TUNISIA

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ABSTRACT. Dental remains of a new hyracoid mammal, *Titanohyrax tantulus* sp. nov., are described from Eocene deposits at Chambi in Tunisia. This new form is one of very few Palaeogene hyracoid occurrences outside the Early Oligocene Jebel Qatrani Formation of Egypt. Very small size and low crown height reflect the primitive nature of the new species relative to other members of the genus. The Chambi rodent fauna and data from charophytes provisionally indicate an early Eocene age for the locality. *T. tantulus* is thus potentially the oldest known representative of the order Hyracoidea.

TODAY the order Hyracoidea consists of only three closely related genera confined to Africa and the Middle East (Olds and Shoshani 1982). In fact, the living forms are the remnants of a Late Miocene radiation which was the last of three major hyracoid diversifications that occurred during the Tertiary (Rasmussen 1989). The first radiation, which is assumed to have started in the Eocene and was confined to Africa, had resulted in a plethora of genera and species by Oligocene times (Meyer 1978; Rasmussen 1989). Unfortunately, due to the paucity of fossil-bearing sediments of early Palaeogene age in Africa, very little is known about the early stages of this radiation. Although four species of hyrax are known from Eocene sites in Algeria (Sudre 1979; Mahaboubi *et al.* 1986) and hyraxes are reported from Palaeogene localities in Libya (Arambourg and Magnier 1961; Savage 1969) and Angola (Pickford 1986), most of our knowledge about the early evolutionary history of this order comes from the Jebel Qatrani Formation of the Fayum Depression in Egypt (Matsumoto 1922, 1926; Meyer 1978; Rasmussen and Simons 1988). Nevertheless, by this time hyraxes were established in a variety of niches as the dominant African herbivores of medium to large body size (Rasmussen and Simons 1988). As the name suggests, *Titanohyrax ultimus* was by far the largest of these Oligocene forms (Matsumoto 1922) and occurs with two slightly smaller species of the same genus within the Jebel Qatrani Formation of Egypt. A somewhat more primitive species, *T. mongereaui*, was reported from the Eocene of Algeria (Sudre 1979), although even at this stage it had already attained great size. We here describe dental remains of a new small hyrax from Eocene deposits in Tunisia which we refer to the genus *Titanohyrax*.

The site from which this material comes is known as the Chambi locality, situated on the northern slope of Jebel Chambi in the Kasserine area of Central Tunisia (Sassi *et al.* 1984; Hartenberger *et al.* 1985). A variety of micromammals have been recovered from lacustrine limestones occurring above a basal conglomerate lying unconformably on marine Late Cretaceous. Insectivores, rodents and primates are presently under study at the Université de Montpellier II (France), while marsupials (Crochet 1986), macroscelidids (Hartenberger 1986) and bats (Sigé 1985) from Chambi have already been reported. The hyrax remains herein described, initially assigned to cf. *Pachyhyrax* and cf. *Saghatherium* in a preliminary report about the locality (Hartenberger *et al.* 1985), are the only macromammals thus far recovered from Chambi. All specimens are registered under the prefix CBI and are housed at l'Institut des Sciences de l'Evolution, Montpellier, France.

Concerning the age of the Chambi locality: known gastropods assigned to *Bulimus* sp. indet. and *Palaeocyclolitus* sp. indet. indicate a broad Palaeocene/Eocene age (Sassi *et al.* 1984). Some 30 m above the lacustrine limestones, charophytes have been recovered which are referrable to the Bartonian *Raskyella* zone of Europe (Sassi *et al.* 1984). It therefore seems possible that the age of this locality could be from Early Eocene to late Middle Eocene. Of three Eocene mammal-bearing

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localities in Algeria, Nementcha is unequivocally of Late Eocene age (Coiffait *et al.* 1984) whereas two other localities, El Kohol (Mahaboubi *et al.* 1986) and Gour Lazib (Sudre 1979), are thought to be of early Middle Eocene age. Based on the observation that rodents from Chambi are clearly more primitive than those from Gour Lazib, Hartenberger *et al.* (1985) suggested an Early Eocene age for this Tunisian locality. Although arguments for the exact age of this locality are at present weak, it is evident that the Chambi fauna is considerably older than the well-known Palaeogene fauna of the Fayum and is plausibly older than the Algerian sites.

SYSTEMATIC PALAEONTOLOGY

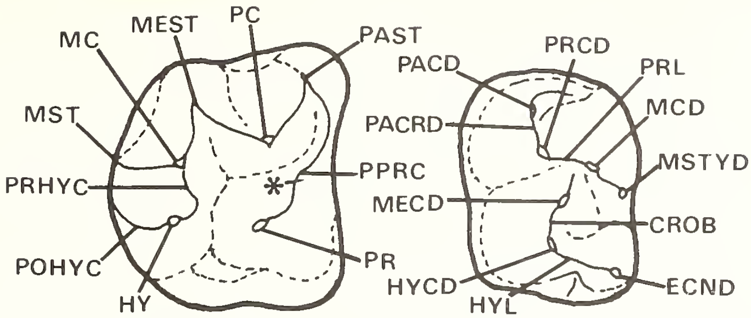
Order HYRACOIDEA Huxley, 1869
Family PLIOHYRACIDAE Osborn, 1899
Genus TITANOHYRAX Matsumoto, 1922

Type species. Titanohyrax andrewsi Matsumoto, 1922.

Remarks. The genus *Titanohyrax* is today considered to contain four species of medium- to large-sized hyraxes (*T. andrewsi* Matsumoto, 1922; *T. mongereaui* Sudre, 1979; *T. ultimus* Matsumoto, 1922; and *T. angustidens* Rasmussen and Simons, 1988). All species except *T. mongereaui* (Sudre 1979) are known only from the Jebel Qatrani Formation of the Fayum Depression, Egypt (Early Oligocene). Early workers failed to recognize *Titanohyrax* as a distinct genus with the result that its constituent species have had a somewhat complex nomenclatural history. Matsumoto (1922) went some way towards clarifying the problem by recognizing that a lower jaw figured by Andrews (1906) as *Megalohyrax minor* and all those specimens treated as *Megalohyrax* by Schlosser (1910, 1911) were in fact distinct from that genus. He then erected the new genus, *Titanohyrax* Matsumoto, 1922, designating four species: *T. ultimus*, based on four isolated and heavily worn teeth, *T. andrewsi* (Andrews' mandibular specimen), *T. palaeotheroides* (Schlosser's *Megalohyrax palaeotheroides*), and *T. schlosseri* (Schlosser's *Megalohyrax eocaenus*). In the most recent wide ranging review of the order Hyracoidea, Meyer (1978) accepted the validity of *Titanohyrax ultimus*. However, he could recognize no morphological or metrical differences between *T. andrewsi*, *T. palaeotheroides* and *T. schlosseri*; thus he synonymized these three taxa under *Titanohyrax andrewsi*. More recently Sudre (1979) referred a very large upper molar from the Eocene of Hammada du Dra (Gour Lazib), Algeria, to the new species, *T. mongereaui*. Finally, based on recent hyracoid finds from the Early Oligocene of Egypt, Rasmussen and Simons (1988) considered Matsumoto's *T. palaeotheroides* to be morphologically distinct from *T. andrewsi*. As Meyer (1978) had already considered the name '*palaeotheroides*' to be a *nomen nudum* due to Schlosser's inadequate description, Rasmussen and Simons (1988) erected the new species, *T. angustidens*.

Although Matsumoto (1922) and Meyer (1978) have given adequate diagnoses of the genus, a short summary highlighting the way in which molar morphology in *Titanohyrax* differs from that of other Palaeogene genera is presented here (see Text-fig. 1. for explanation of terminology).

Titanohyrax differs from *Geniohyus*, *Bunohyrax* and *Pachyhyrax* in its possession of complete lower molar protolophid and hypolophid and a well-differentiated metastylid. Upper molars further differ from those of both *Geniohyus* and *Bunohyrax* in their possession of more selenodont buccal cusps and trenchant parastyle and mesostyle, and from those of *Pachyhyrax* by the very reduced prehypocrista, absence of spurs on the distolingual surface of the paracone and mesial surface of the distal cingulum. *Saghatherium* differs dramatically from *Titanohyrax* with its absence of lower molar metastylid, very strong prehypocrista, well-developed ribs on the buccal side of both the paracone and metacone and distinctive spurs on the lingual side of very prominent metastyle and mesostyle. Although the lower molars of *Thyrohyrax* possess a metastylid, the entoconid differs from *Titanohyrax* in being mesially very extensive, almost closing the valley between it and the metaconid. In addition, *Thyrohyrax* can be distinguished from *Titanohyrax* in its possession of a very extensive upper molar prehypocrista and folded buccal wall of the protocone. *Titanohyrax* has



TEXT-FIG. 1. Schematic drawing of hyracoid molars showing points of occlusal morphology referred to in the text. Right upper M2 (left) and right lower M2 (right). Orientation: Mesial towards right, buccal towards top (left) and mesial towards top, buccal towards left (right). The following morphological features are illustrated: CROB, cristid obliqua; ECND, entoconid; HY, hypocone; HYL, hypolophid; MC, metacone; MCD, metaconid; MECD, mesoconid; MEST, mesostyle; MS, metastyle; MSTYD, metastylid; PACD, paraconid; PACRD, paracristid; PAST, parastyle; PC, paracone; POHYC, posthypocrista; PPRC, preprotocrista; PR, protocone; PRCD, protoconid; PRHYC, prehypocrista; PRL, protolophid. The asterisk marks the 'paraconular' swelling of the preprotocrista.

most often been confused with *Megalohyrax*. However, unlike *Titanohyrax*, the lower molars of this genus have no metastylid and paraconids tend to be well developed. In the upper molars, buccal styles tend to be rounded and not trenchant with much stronger development of the metastyle. The hypocone and protocone are much more similar in size, and although the protocone lacks a postprotocrista the prehypocrista is much more prominent than in *Titanohyrax*.

Titanohyrax tantulus, sp. nov.

Text-figs 2–3

1985 cf. *Pachyhyrax* and cf. *Saghatherium* Hartenberger *et al.*, p. 649.

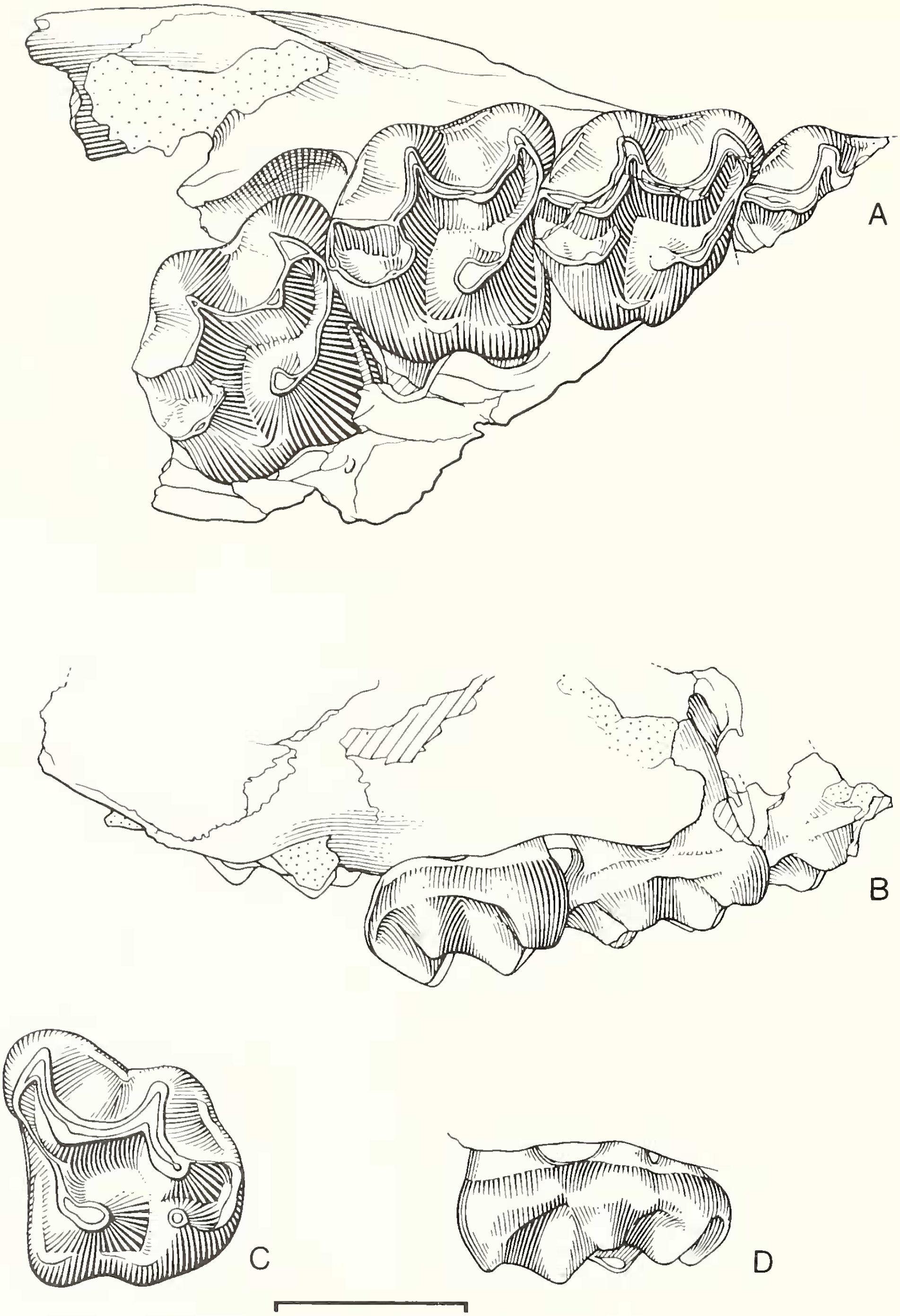
Holotype. CBI 42 right juvenile maxillary fragment with a fragment of DP3 and complete DP4-M2 (Text-fig. 2A–B).

Hypodigm. CBI 27, isolated upper left M3 (Text-fig. 2C–D), CBI 42, lower right M2 (Text-fig. 3A–B), CBI 43, lower left ?molar/premolar (Text-fig. 3C–D), CBI 41, lower right I1 (Text-fig. 3E–F).

Locality and horizon. Northern flank of Jebel Chambi close to Kasserine, Central Tunisia. The Eocene Chambi Formation lies unconformably on marine Late Cretaceous. Specimens come from a 2 m thickness of lacustrine limestone lying about 30 m above the basal unconformity.

Etymology. *Tantulus* (Latin), meaning quite little and referring to the small size of this species relative to other members of the genus.

Diagnosis. *T. tantulus* sp. nov. differs most dramatically from the four previously reported species in its much smaller size, and from all except *T. mongereaui* by its very low crown height and basally rounded upper molar styles. Morphologically it differs from *T. ultimus* by its greater differentiation of a metastylid, absence of entostylar development and stronger buccal cingulid. With the exception of size and degree of hypsodonty the lower molars of *T. andrewsi* are probably most similar to *T. tantulus*, although this species still exhibits some minor development of an entostylid. *T. angustidens* is the most distinct member of the genus possessing well-developed upper molar metastyles and long narrow lower molars with extended trigonids. In the possession of a preprotocrista that extends to



TEXT-FIG. 2. *Titanohyrax tantulus* sp. nov. A, CBI 42 right maxilla with fragment of DP3, and DP4-M2 in occlusal view. B, the same specimen in buccal view. C, CBI 27 upper left M3 in occlusal view. D, same specimen in buccal view. Scale = 10 mm.

the parastyle and carries a paraconular swelling, *T. tantulus* is similar to *T. mongereaui*, although it differs from this and all other species in that the buccal side of the paracone is slightly convex as opposed to concave. The absence of entostylar development and the occurrence of a small mesoconid on the cristid obliqua of the lower molars are distinguishing features not reported in any other species of the genus.

Description. The type is a well-preserved portion of a right maxilla from a young individual (Text-fig. 2A–B). DP4 and M1 are in place with M2 erupting from the crypt behind. Morphology from DP4 to M2 is unchanged although there is a normal increase in size distally. The molars are very low-crowned and somewhat trapezoidal in outline, with slightly oblique ectolophs; the width being slightly greater than the length. The parastyle is very strong and marks the most buccally extensive part of the tooth. The mesostyle is strong and compressed mesiodistally near its apex but, in common with the parastyle, becomes more globular towards the base of the tooth. Both the paracone and metacone are lingually displaced with respect to the buccal styles giving the ectoloph a very selenodont appearance. Buccally, the wall of the paracone is slightly convex while that of the metacone is flat. The metacone is more lingually positioned than the paracone, lying lingual and only slightly distal to the mesostyle. A very short postmetacrista descends abruptly in a distal and slightly buccal direction from the summit of the metacone to join the distal cingulum, thus there is no real development of a metastyle.

TABLE 1. *T. tantulus* sp. nov. length (L) and width (W) measurements (mm) of dental specimens referred to in the text.

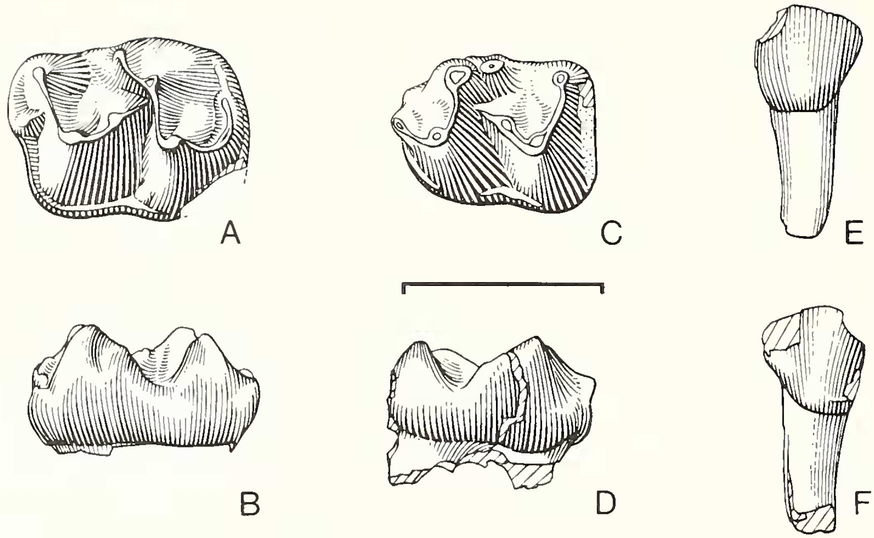
	DP4		M1		M2		M3	
	L	W	L	W	L	W	L	W
Upper teeth								
CBI 42	9·9	10·1	11·1	12·1	11·7	12·4	—	—
CBI 27	—	—	—	—	—	—	12·3	13·0
Lower teeth								
CBI 44	—	—	—	—	11·6	9·2	—	—
CBI 43	—	—	?10·2	6·2	—	—	—	—

The protocone is by far the more dominant of the two lingual cusps. It is situated slightly more distally relative to the paracone such that its mesial face slopes shallowly towards the mesiolingual corner of the tooth. The preprotocrista is exceedingly well developed; it extends mesiobuccally to join a lingually trending crest from the apex of the parastyle. At a point midway between the protocone and paracone the preprotocrista is slightly raised to form a small paraconular swelling. There is no development of a postprotocrista. The hypocone is much smaller than the protocone, being mesiodistally compressed and confined to the distolingual corner of the tooth. The prehypocrista is extremely short, buccally directed and abuts the base of the lingually displaced metacone. Descending distally from the hypocone, the short posthypocrista swings abruptly towards the buccal side of the tooth to join the short postmetacrista, thus providing the slightly convex closure to a small distal fossette. Cingula are disjunct around the base of the tooth, being present only at the buccal base of the paracone and metacone, around the mesiolingual base of the protocone and between the protocone and hypocone.

An isolated left upper M3 (Text-fig. 2C–D) is somewhat more trapezoidal in outline. The preparacrista is a little longer and more buccally directed while the hypocone is even more constricted than in the more anterior molars and shows no development of a prehypocrista.

The lower dentition is known only from three isolated teeth. Two molariform teeth are interpreted here as a right M2 (Text-fig. 3A–B) and smaller left M1 or molariform premolar (Text-fig. 3C–D). In addition a single spatulate incisor is known. Spatulate lower incisors were cited as a titanohyracid character by Rasmussen and Simons (1988) in their diagnosis of the genus. Moreover, since *T. tantulus* is the only macromammal known from the Chambi locality this isolated incisor is confidently referred to this species. From the degree of asymmetry it appears to be a right first incisor (Text-fig. 3E–F).

The second molar is essentially bilophodont with strong transverse crests joining the protoconid to the metaconid mesially and the hypoconid to the entoconid distally. A short paracristid descends steeply from the



TEXT-FIG. 3. *Titanohyrax tantulus* sp. nov. A, CBI 44 lower right M2 in occlusal view. B, same specimen in lingual view. C, CBI 43 lower left ?M1 or P4. D, same specimen in lingual view. E, CBI 41 lower right I1 in buccal view. F, same specimen in lingual view. Scale = 10 mm.

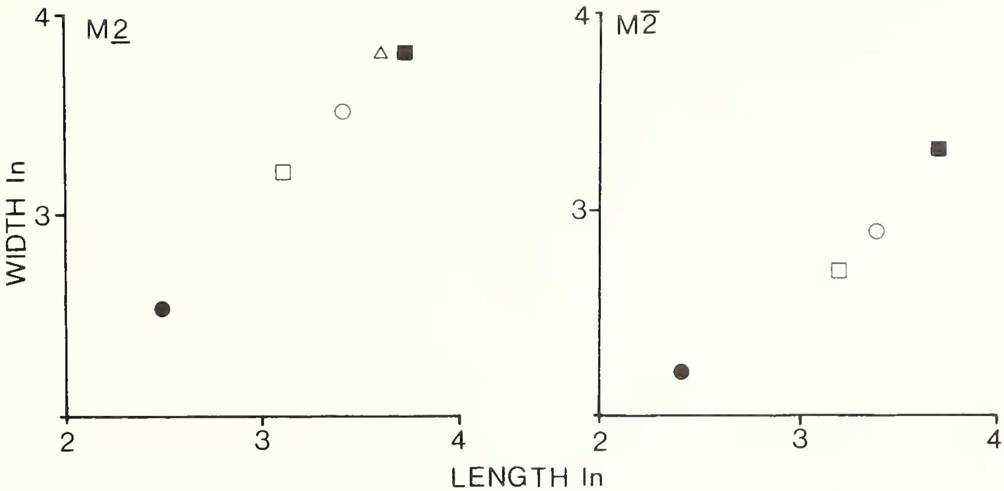
protoconid, curving mesiolingually to merge low down with the mesial cingulum. A very slight swelling of the paracristid occurs just in front of the protoconid and could be interpreted as a vestigial paraconid. The anterior part of the trigonid is greatly reduced and correlates with the poor development of the postmetacrista and virtual absence of a metastyle in the upper molars. The metaconid is well developed and situated almost directly opposite the protoconid. A distinct distolingually trending crest descends a short distance from the summit of the metaconid to end in a prominent metastylid. In the distal part of the tooth, the strong hypolophid is slightly obliquely set due to the somewhat more mesial position of the hypoconid with respect to the entoconid. From the summit of the hypoconid a strong cristid obliqua descends mesiolingually to terminate just buccal of the metaconid base. Just before its termination, there is a small but discrete swelling on the cristid obliqua, more easily visible in lingual view, which is here termed a mesoconid. Cingula are quite well developed on all but the lingual base of the tooth. Distally a crest descends steeply from the back of the entoconid to form a buccally descending distal cingulum. At about the middle of the distal cingulum, a small spur-like hypoconulid is appressed to the distal base of the hypolophid.

The smaller molariform lower tooth is somewhat narrower relative to length than that already described. In addition it exhibits a stronger more mesially directed paracristid terminating in a distinct paraconid, the metastylid is more distally positioned than in the bigger tooth and the buccal cingulum is much weaker and is interrupted around the protoconid and hypoconid.

DISCUSSION

The following features of *T. tantulus* are typical of the genus *Titanohyrax*.

1. Highly selenodont buccal cusps lacking both buccal and lingual ribs with at least proximally trenchant parastyle and mesostyle. Very little development of a metastyle.
2. Protocone much larger than hypocone with strong preprotocrista and no postprotocrista.
3. Hypocone small, mesiodistally compressed with very short recurved prehypocrista abutting the lingually displaced metacone. Short posthypocrista forming the distal cingulum.
4. Mesiodistal compression of the lower molar trigonid basin.
5. Strongly developed metastylid.
6. Spatulate rather than tusk-like lower incisors.



TEXT-FIG. 4. Bivariate plot of upper (left) and lower (right) M2 (log length against width) of species attributed to the genus *Titanohyrax*. Closed circles = *T. tantulus* sp. nov. (measurements in Table 1); open circles = *T. andrewsi* (measurements taken from Matsumoto 1926); closed squares = *T. ultimus* (measurements taken from Matsumoto 1922); open squares = *T. angustidens* (measurements taken from Rasmussen and Simons 1988); open triangle = *T. mongereaui* (measurements taken from Sudre 1979).

The specimens herein described differ most dramatically from all other known members of the genus *Titanohyrax* by their extremely small size (Text-fig. 4). This alone is a sufficient criterion to warrant the erection of a new species. In addition, the upper teeth are very brachyodont with basally rounded styles, features that can be interpreted as primitive with respect to the much more hypsodont Fayum species. Indeed, the much sharper buccal parastylar and metastylar crests in Fayum forms are likely to be a simple correlate of their increased crown height. Further, there are several features observable in this material which have not been reported in previous diagnoses of the genus. The first concerns the great extent of the preprotocrista which is continuous with the buccally directed fold of the parastylar apex. In addition, the preprotocrista exhibits a small 'paraconular' swelling before joining the parastylar crest. Sudre (1979) emphasized both of these features in his description of *Titanohyrax mongereaui* from Algeria. This is also a very brachyodont form with rather globular upper molar styles; however, *T. mongereaui* is more than three times as large as the form from Chambi. In the lower molars, the presence of a small mesoconid on the cristid obliqua has never been reported for the genus although lower molars of *T. mongereaui* are as yet unknown.

As the larger lower molar occludes well with the upper molars, something of the occlusal relationship between the teeth can be deduced. In buccal phase, the metaconid occludes with the mesial face of the protocone while the metastylid occludes with the mesiolingual face of the protocone. The raised edge of the 'paraconular' swelling therefore passes between the protoconid and metaconid to shear against the protolophid. At the end of this phase of occlusal motion, the mesoconid of the cristid obliqua comes to lie in the depression between 'paraconular' swelling and protocone. Recent research has strongly proposed a close phylogenetic linkage between hyraxes and the order Perissodactyla (Fischer 1986; Prothero *et al.* 1988). Although early perissodactyls exhibit well-defined upper molar paraconules, these are always related occlusally to the development of the metastylid (Hooker 1989). Since this is not the case in *T. tantulus*, neither the 'paraconular' swelling nor the metastylid can be homologized with the condition observed in perissodactyls.

Since the 'paraconular' swelling and continuity of the preprotocrista with the parastyle has only been demonstrated explicitly in the huge brachyodont *T. mongereaui* from the Middle Eocene of

Algeria (Sudre 1979), it is tempting to postulate a close phylogenetic link between it and *T. tantulus*. The question as to whether the great disparity in size (Text-fig. 4) reflects phyletic size increase between the two species or an adaptive radiation must, however, remain open; nevertheless, if the data from rodents and charophytes indicating an Early Eocene age for the Chambi locality is substantiated, the former would be a reasonable first hypothesis.

CONCLUSIONS

The discovery of a new diminutive titanohyracid from Eocene deposits of Tunisia extends both the temporal and geographical range of the mammalian order Hyracoidea and increases the size range within the genus *Titanohyrax* substantially. The degree of brachyodonty, relative to Fayum members of the genus, indicates that the Tunisian species is more primitive. Moreover, the suggested Early Eocene age for the Chambi locality (Hartenberger *et al.* 1985) would place *T. tantulus* as the oldest representative yet known of the order Hyracoidea.

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